Male aggression varies with consortship rate and habitat in a dolphin social network

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ABSTRACT

Coalitions and alliances exemplify the core elements of conflict and cooperation in animal societies. Ecological influences on alliance formation are more readily attributed to within-species variation where phylogenetic signals are muted. Remarkably, male Indo-Pacific bottlenose dolphins in Shark Bay, Western Australia, exhibit systematic spatial variation in alliance behavior, not simply within a species or population, but within a single social network. Moving SE-NW along Peron Peninsula in Shark Bay, males ally more often in trios than pairs, consort females more often, and exhibit greater seasonal movements. Ecological models predict more male-male conflict in the north, but sufficient observations of aggression are lacking. However, dolphins often incur marks, in the form of tooth rakes, during conflicts. Here we report that the incidence of new tooth rake marks varies systematically in the predicted pattern, with greater marking in the north, where males form more trios and consort females at a higher rate. While our previous work demonstrated that alliance complexity has an ecological component, we can now infer that ecological variation impacts the level of alliance-related conflict in Shark Bay.

KEY WORDS

Aggression, wounds, reproductive strategy, competition, cetaceans, coalitions

SIGNIFICANCE STATEMENT

To understand ecological influences on animal societies, researchers have focused on differences within species, where confounds due to evolutionary history are minimized. Such differences are usually found among geographically separated populations, but in Shark Bay,

Western Australia, male dolphin alliance size and access to females increases along a spatial axis within a single social network. Here we report that aggression levels, evidenced by tooth rake marks, increase along the same axis. Alliances are of particular interest as they represent a complex kind of relationship, often implicated in the evolution of social intelligence. Our discovery of spatial variation in alliance behavior and aggression within a social network provides a unique opportunity to investigate the intersection of cognition, social structure, and ecology.

INTRODUCTION

Conflict over resources is an inevitable consequence of group formation and, along with cooperation, is key to understanding animal societies. Animals may cooperate in conflict by forming coalitions and alliances, which are relatively common within mammal social groups compared to other taxa (Harcourt and de Waal 1992). Alliance relationships within groups may become very complex when individuals use affiliative interactions to form and compete for allies, and hence may have influenced the evolution of cognitive abilities and brain size (e.g. Chapais 1995).

The Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) of Shark Bay, Western Australia, form the most complex alliances known outside our own species (Connor 2007; Connor and Krützen 2015). Males cooperate in pairs and trios (1^{st}-order alliance) to consort individual females (see Online Resource 1), and most males belong to a group of 4-14 males (2^{nd}-order alliance) that cooperate in conflicts with other groups (Connor and Krützen 2015; Connor et al. 1992). Particular 2^{nd}-order alliances associate preferentially and cooperate against other groups, forming a third alliance level (Connor et al. 2011). Aggression has been studied primarily in consortships, in which males herd females using threats and direct aggression, and in fights between 2^{nd}-order alliances (Connor et al. 2011; Connor and Krützen 2015). Dominance relationships are found in captive bottlenose dolphins (Samuels and Gifford 1997) and, in Shark Bay, they are suggested by the positive relationship between the rate that males consort females and the stability of their 1^{st}-order alliances (Connor and Krützen 2015).

In contrast to Shark Bay, male bottlenose dolphins (*Tursiops truncatus*) in Sarasota, Florida, form pairs but not trios and higher alliance levels are not evident (Owen et al. 2002). It is difficult to ascribe these differences to ecological variables alone because, in addition to their phylogenetic distance, the populations differ in body size, sexual size dimorphism, and

77 female reproductive schedules, all of which may impact selection for alliance formation
78 (Connor et al. 2000). Such problems, as well as strong phylogenetic signals in comparative
79 analyses (Thierry 2008; Clutton-Brock and Janson 2012), have increasingly shifted the search
80 for ecological influences on social structure to variation within species (Chapman and
81 Rothman 2009; Strier 2009; Maher and Burger 2011; Kappeler et al. 2013; Schradin 2013).
82 Typically, such variation in social structure is reported from geographically separated
83 populations, which differ in their ecology (Kappeler et al. 2013; for an exception see
84 Rubenstein 1981).

85 Therefore, our recent report of systematic spatial variation in alliance behavior in Shark Bay,
86 not in geographically separated populations but within a single social network, was surprising
87 (Connor et al. 2017). Participation in male trios (versus pairs), the extent of seasonal range
88 shifts, and consortship rates all increased from Southeast (SE) to Northwest (NW) along the
89 50 km length of the study area. No model of random demographic variation or culture can
90 explain the systematic spatial variation in alliance size and the rate males consort females
91 (Connor et al. 2017). Ecological models, including predation risk, resource distribution, and
92 the "rate of interaction" model predict, or are consistent with, greater levels of aggression in
93 the north where males form trios and consort females more frequently.

94 *The rate of interaction* model (Connor and Whitehead 2005, see also Whitehead and Connor
95 2005), shows that alliances will form, or become larger, when individuals encounter each
96 other more often in competitive circumstances. It is self-evident that aggression is predicted
97 to be more frequent when males are interacting at a higher rate in conflict over resources.
98 Males may form larger alliances to reduce the *risk of predation* through predator detection,
99 dilution, or cooperative defense. A cost of such grouping would be greater conflict over
100 females and other resources, leading to more frequent aggression. The *distribution of*
101 *resources* may impact aggression levels if, for example, a greater abundance of schooling fish

in the NW habitat favored larger alliances by reducing grouping costs (compared to the SE if males there feed more on solitary fish or smaller schools of fish). Greater levels of competition, and hence aggression, could be tolerated in the NW if males derive sufficient foraging benefits from each other, such as detection, defense, or cooperative herding of schooling fish. We currently have no evidence for any of these factors.

Direct observations of aggressive interactions between bottlenose dolphins in the field are infrequent but patterns of wounding resulting from intraspecific conflict may be a useful proxy. This is demonstrated in studies of terrestrial mammals, which often concluded that adult males acquire wounds at significantly higher rates than other age-sex classes, and authors have inferred that males may increase their reproductive fitness by fighting for access to females (Whitten and Smith 1984; Ruehlmann et al. 1988; Drews 1996; MacCormick et al. 2012; Charpentier and Drea 2013).

The most serious form of aggression in all cetaceans is delivered with blows from the flukes and peduncle, which do not generally leave external marks (Connor et al. 2000). Odontocetes often use their teeth as weapons in conflicts, leaving visible tooth rake marks on the skin (e.g. Ross and Wilson 1996). In species with teeth modified for use as weapons, wounds can be deep, long-lasting, and perhaps lethal (Gerson and Hickie 1985; MacLeod 1988). Most delphinids possess small teeth adapted for grasping rather than tearing or crushing prey, so while they are unlikely to cause serious wounding they are commonly used in fighting. Several studies have examined tooth rakes in delphinids, including bottlenose dolphins (Scott et al. 2005; Martin and Da Silva 2006; Rowe and Dawson 2009; Marley et al. 2013; Brown et al. 2015; Orbach et al. 2015; Lee et al. 2019). These studies found significantly higher rake marks in males than females (but see Tolley et al. 1995).

Given that adult male dolphins in Shark Bay form larger alliances and consort females at higher rates from SE to NW in the study area, aggression should also increase along this trajectory. Here we test this prediction by examining 'new' tooth rake marks, a reliable indicator of recent aggressive interactions (see Online Resource 1).

METHODS

Study site, subjects and observations.

Over 1,500 resident dolphins off the eastern side of Peron Peninsula, which bisects Shark Bay, Western Australia, have been individually identified and observed since the mid-1980s (Connor and Krützen 2015). The habitat changes distinctly along the 50km length of study area, from NW to SE. Coastal shallows of the peninsula sloping to a broad, open habitat characterize the NW study area, while the SE area consists of shallow banks interspersed with deeper channels.

From 2001-2006, we studied the behavior of 121 male dolphins in this population (Connor et al. 2011; Randić et al. 2012; Connor et al. 2017). Male association, behavioral, and ranging data were collected during dolphin group surveys (at least five minutes) and focal follows (at least one hour, but typically three to four hours) during the same five-month period each year (July-November), the last three of which are the peak breeding season (Austral spring). During all encounters, photographs of dorsal fins were taken to determine group composition. It was not possible to record data blind because our study involved focal animals in the field.

Photo Analysis.

From 3,816 dorsal fin images reviewed, those of 95 individual males were of sufficiently high quality for the study (see Online Resource 1). Of these 95 individuals, 86 males associated in twelve 2nd-order alliances and nine males belonged to five trios that were not part of a 2nd-order alliance (Connor et al. 2011). Percent area of the dorsal fin covered by new tooth rake marks, recognized as non-pigmented lines with ragged edges (See Fig. S1 for examples of healing stages), was calculated using GIMP software (http://www.gimp.org) in which the total pixels of both new tooth rake area (determined by drawing a complex polygon around the rake lines) and the total fin area were calculated. Only the best left and/or right photograph (see Online Resource 1) per year for each individual was used for calculating new tooth rake coverage, resulting in possible data values for analysis from 595 photographs. The best left and right sides of the fin of the same animal in a year were then averaged together.

Statistical Analysis.

For all analyses, year was a confounding variable in the data. The number of pictures rated as high-quality did not vary significantly between years (Chi-squared test: df = 5, $p = 0.21$); meaning that the detection of scarring on photos increased with year. Among high-quality photos selected for analysis, there was a range in the ability to accurately detect new scarring. We suspect that the upgrades and technological advancements in cameras, changes in camera settings, number of pictures taken, and perhaps user skill with those cameras, caused tooth rakes to be more visible in high-quality photos from later years (Online Resource 1). To remove this effect, the most recent available data-point of each male was pulled from those available (n = 95). Since the calendar month photos were taken was not correlated with alliance home-range centroid position (Kruskal-Wallis test by ranks : df = 7, $p = 0.6073$) (Fig. S2) or directly with new rakes (Kruskal-Wallis rank sum test: df =7, $p = 0.3872$), using this subset of data minimized the effect of year on models.

Second-order alliance stability was calculated as in Connor et al. (2011), defined as 100 × $1 – &'()**+,+- 011)0 2+378. All alliance home-range centroid and consortship rates were '24-34,.35)63 calculated as in Connor et al. (2017). Briefly, centroids were calculated using one sighting per day per individual (mean 43.1 sightings per individual; range 6-69, median 40). Then, first daily sightings for all individuals within the same 2nd-order alliance were combined to determine a 2nd-order alliance centroid (mean 381 sightings per 2nd-order alliance; range 135-915, median 339). Alliance centroids fell approximately on a NW-SE line parallel to the coast, described by a least-squares best-fit line. An ordinal rank, as well as continuous metric position, along this best fit line was calculated for each centroid, increasing in the SE direction (see Connor et al. 2017). Individual consortship rate was calculated as the number of days a male was seen consorting a female, divided by the total number of days that male was observed during the study period (Connor et al. 2011).

A Wilcoxon rank-sum test was used to compare the percent coverage of new tooth rake marks of members of 2nd-order alliances with males in lone-trios. For all alliance males, ANOVA type II tests were used to investigate the relationships of new rakes to alliance size, stability, and home-range centroid. To examine the relationship between consortship rate and new rakes, a generalized linear mixed model (GLMM) with a quasi-Poisson distribution was performed, including alliance membership as a random effect on the intercept using the R package nlme (Pinheiro et al. 2013), and an R^2_{GLMM} value was calculated following Nakagawa and Schielzeth (2012). To evaluate within-alliance differences in new tooth rake coverage, the individuals with the highest and lowest consortship rate in each alliance were compared using Welch's two-sample t-tests. All statistics were performed in R 3.3.1 (R Core Team 2017).

Data availability

Data analysed in this paper are presented in Online Resource 1 (Table S3).

RESULTS

There was a significant decrease in new dorsal fin rakes from NW to SE using the ordinal rank of 1-12 for alliances (ANOVA: $F(1,84) = 5.88$, $p = 0.017$), and the metric distances (ANOVA: $F(1,84) = 4.17$, $p = 0.044$) (Fig. 1). New rakes and consortship rate were significantly correlated (GLMM: t value = 2.84, p =0.0059, $R^2_{GLMM} = 0.092$) (Fig. 2). Second-order alliance members had significantly higher new tooth rake marking than lone-trio males (Wilcoxon rank-sum: $W = 564$, $p = 0.025$) (Fig. S3). Second-order alliance identity was not significantly related to new rakes (ANOVA: F(11,74) = 1.90, df = 74, $n = 86$, $p = 0.053$) (Fig. S4). There was also no significant relationship between new rakes and alliance size (ANOVA: df = 84, $n = 86$, $p = 0.45$) or stability (ANOVA: df = 84, $n = 86$, $p = 0.41$), nor a significant difference in raking between males with the highest and lowest consortship rate within each alliance (Welch's two-sample t-tests: $p = 0.74$). See Table S2 for model details and Table S3 for raw data.

DISCUSSION

Previously, we showed that consortship rate and trio (versus pair) formation increased from SE to NW in our study area on the east side of Peron Peninsula in Shark Bay (Connor et al. 2017). This discovery of systematic spatial variation in alliance behavior was unprecedented. Here we add a key element to this discovery by showing that the extent of new marks from aggressive interactions increases in the same manner along the peninsula, indicating more intense competition in the north. Increased rake marks could be explained by increased conflict between, or within and between, 2^{nd}-order alliances.

We assume here that the differences in new tooth rakes along the peninsula are due to differences in aggression among males. We cannot assume that all tooth rake marks are made by males but know of no model that could explain our results based on differences in aggression by females toward males, independent of differences in the level of conflict between males.

Using tooth rake marks to assess variation in aggression received among individuals is potentially problematic. In primates, wound healing can be impacted by an individual's sex, age, reproductive effort, nutritional state, and recent injury history (Archie 2013). Several studies have also revealed a complicated relationship between wound healing and stress (Christian et al. 2006; DeVries et al. 2007; Martin 2009). For some species, positive social bonds induce faster healing (Detillion et al. 2004). Alpha male baboons, for example, heal faster than lower-ranking males (Archie et al. 2012). Such variability in wound-healing between individuals can skew results of studies based on overall wound patterns.

The relatively quick re-pigmentation of tooth rake marks in dolphins (Online Resource 1) allows us to compare injuries of similar temporal range. Importantly, our results demonstrate differences in new rakes along a spatial axis rather than among individuals in an area based on individual differences in rank, sex, etc., as described in primates. Factors such as age and sex should not vary systematically along the spatial axis upon which we found an increase in new rakes; however, we can ask if nutritional or social stress might vary systematically along this axis. In the SE of our study area, individual males are more often in pairs, have lower consortship rates, and less new tooth rakes. The SE habitat may be marginal for this population (Connor et al. 2017) but if the males there are nutritionally stressed, healing rates should be slower. Equal levels of conflict but slower healing rates in the SE should therefore produce a higher percentage of rakes in the SE. Males in the NW consort females at higher rates and more often in trios. Thus, if the greater incidence of wounding in the NW owes to

slower healing due to higher stress levels among males in the area, the stress would be due to greater social conflict, rather than nutritional stress.

A range of ecological variables could impact the rate that males come into conflict over estrous females, including population density, ranging patterns, detection distance, food distribution and abundance, and predation risk (see Connor et al. 2017). The greater seasonal range shifts of the NW alliances could bring them into contact with more, as well as less familiar, alliances than males in the SE that may interact with the same groups year-round. Both factors could increase aggressive interactions for NW males.

The correlation between new rakes and consortship rate supports the hypothesis that more reproductively successful males engage in more agonistic interactions. The greater occurrence of new rakes in 2nd-order alliance males compared to lone-trio males is expected considering lone-trio males in this study were older and rarely observed with female consorts (Connor et al. 2011), the usual source of male-male conflict in this population. Similarly, in male olive baboons (*Papio anubis*), wounding was more prevalent in reproductively successful males (using rank as a proxy), due to more frequent aggressive encounters (MacCormick et al. 2012).

There may be links between social status and wounds in dolphins, as have been reported in some terrestrial mammals, but these relationships have not yet been demonstrated in an odontocete. Such relationships may be difficult to detect in Shark Bay dolphin alliances, given the nested structure of the alliances and that aggression occurs within and between all three alliance levels (Connor and Krützen 2015). Wounding rates are inversely related to rank in stump-tailed macaques (*Macaca arctoides*) (Whitten and Smith 1984). If the Shark Bay dolphins followed a similar pattern, we would have expected to find greater coverage of new tooth rakes in dolphins with the lowest consortship rates within alliances compared to those with the highest rates, but we did not. A relationship between rakes and rank (or some other

measure of competitive ability within alliances) may simply not exist or it may be obscured by wounds higher ranking males receive if they participate more in conflicts between 2nd-and 3rd-order alliances.

The systematic spatial variation in alliance behavior that we have discovered here (and in Connor et al. 2017) demonstrates that the complexity of male alliances in this population has an ecological component. Given that alliances within social groups may be the most cognitively demanding type of social relationship (Chapais 1995) and that the Shark Bay dolphins exhibit the most complex alliances known outside of humans (Connor 2007), we are presented with a unique opportunity to examine the intersection between cognition, social complexity, and ecology.

COMPLIANCE WITH ETHICAL STANDARDS

ETHICAL APPROVAL

Data were collected under permits from the Western Australian Department of Parks and Wildlife. The University of Massachusetts at Dartmouth and the University of New South Wales provided animal ethics approvals for this study. All applicable international, national, and/or institutional guidelines for the use of animals were followed.

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COMPETING INTERESTS

The authors declare no competing interests.

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408

409 FIGURE AND TABLE CAPTIONS

410 **Fig. 1** Percent fin area covered in new tooth rake marks for alliance-member males (n = 86),
411 by alliance home-range centroid, plotted as an ordinal rank from Northwest (1) to Southeast
412 (12). Line of best fit, p = 0.01741. The boxes show the median, interquartile range, and
413 whiskers (Q1-1.5xIQR and Q3+1.5xIQR). Circles represent outliers.

414 **Fig. 2** Percent fin area covered in new tooth rake marks and consortship rate for alliance-
415 member males (*n* = 86). Generalized linear model with alliance as random effect, *p* = 0.0059.
416 Different colours represent different 2nd-order alliances.

417